Cortical Cell Lamination of the Hemispheres of Papio Hamadryas.

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With Plates 24-30.

PREFACE.

THE localisation of function in the cerebral cortex is a problem on the importance of which it is hardly necessary to dwell. Its practical value to the surgeon and its theoretical interest to the physiologist and psychologist are obvious and have been sufficiently recognised. It is a problem which concerns many of the biological sciences, since it can be approached in many different ways. The physiologist has, by the electric stimulation of different parts of the surface of the brain in various animals, obtained responses from different parts of the body, and has thus been enabled to say what areas control the movements of the various groups of muscles. Occasional opportunities are afforded to the surgeon for making similar experiments on the human subject. The ablation of different parts of the cerebral cortex in the living animal is another physiological method from which valuable conclusions have been drawn. Observations on the alterations in function associated with local cortical lesions due to accident or to disease form a parallel method of research in the domains of pathology.

The contribution called for from the anatomist and histo-

logist is the mapping out of the cortex into areas differing from one another in structure. In doing this he may take into account the form and arrangement either of the nerve-cells or of the nerve-fibres, or he may divide the surface into regions distinguished by the period at which they arrive at maturity. In an exhaustive treatment of the subject evidence obtained in all these ways must be considered and co-ordinated —a difficult task, since the interpretation of the observations is beset with pitfalls, and in consequence a number of apparent inconsistencies have to be explained away or harmonised.

On some points already a considerable degree of certainty has been arrived at, namely the extent of the area concerned directly with the movement of the voluntary muscles, and of that region in which the visual impulses set up in the retina reach the cortex. With regard to these points the evidence from all sources is in agreement, and the definite function is in each case correlated with a perfectly definite structure, which, particularly in the case of the visual area, sharply delimits it. A perfectly definite structure also marks the olfactory cortex, while to many other structurally distinct areas a special function may be assigned with some degree of confidence.

That a better appreciation of a physiological and anatomical problem may be obtained by extending it into the realms of comparative physiology and comparative anatomy is generally accepted. Both the points of agreement and the points of divergence in structure between animals with different habits living in different environments may elucidate the relation between structure and function. The present paper aims at making a small but definite contribution to the subject, in that it consists of a description of a special aspect of the histology of the cortex in an animal not hitherto treated in this way. The histological study of the cortex may be pursued in at least three different ways. Firstly, the nerve-fibres may be stained by some method like that of Weigert; secondly, the nerve-cells may be stained either by the Golgi or Cajal process. These are uncertain in action and only

select a few cells for staining, but show them complete with
dendrites and axon, and may enable one to trace for a con-
siderable distance the path of the latter, in some cases even
as far as its terminal arborisation. These methods are of
great importance, and throw light on the relations of one cell
to another within a particular cortical area, and thus on the
individual functions of the different types of cell. They are,
however, unsuitable for the survey of the arrangement of the
cells in their several layers, which is necessary in order to
divide the cortex into regions according to the type of cell
lamination present in each. For this purpose it is necessary
to employ a method of a third type, such as that of Nissl, in
which every cell is rendered visible by the stain. Nissl's
method shows the general shape of each cell and its principal
dendrites, also the structure of the nucleus and the arrange-
ment of the extra-nuclear chromatin ; it does not show the
axon nor the nerve-fibrils running through the body of the
cell.

It is a variation of Nissl's methylene-blue which has been
used for the purposes of the present paper, namely Unna's
polychrome methylene-blue, as the particular point dealt with
is the arrangement of the layers. Much work of the kind
has been done on the human brain, without, however, exhaust-
ing the subject, but the other Primates have been somewhat
neglected. Of the few papers dealing with them the earliest
is that of Schlapp (' Archiv f. Psychiat.,' Bd. xxx), " Der
Lebenbau der Gross linn rinde des Affen Macacus cyno-
mologus." Schlapp does not go into any great detail :
three types only of cortex are described and somewhat
roughly figured, their extent being shown by a sketch of the
lateral surface of the hemisphere.

Campbell (' Histological Studies on the Localisation of
Cerebral Function,' Cambridge, 1905) describes the brains
of the chimpanzee and orang-outang. This work, which fills
a volume of considerable size, deals principally with the
human brain, and treats the subject with praiseworthy
thoroughness. Not only is the arrangement of the cells

described, but that of the fibres also. The human brain is
compared with that of the two apes, and the clinical, patho-
logical, and experimental evidence is fully discussed in its
relation with the histological results.

An excellent series of papers on the cell lamination have
been published by Brodmann in the 'Journal f. Psychologie
und Neurology,' 1903 and onward, and summarised in his
book, 'Vergleichende Lokalisations lehre der Grosshimrinde,'
Leipsig, 1909. The human brain is described in great detail,
a very large number of separate areas (more than fifty) being
distinguished histologically. Similar detailed descriptions of
the brains of Cercopithecus and of the lemurs are given, while
the marmoset (Hapale) is dealt with more shortly. The homo-
logies between different regions in the human and other
Primate brains are dealt with as far as possible.

Mott and Kelley publish a "Complete Survey of the Cell
Lamination of the Cerebral Cortex of the Lemur" ('Proceed-
ings of the Royal Society,' B., vol. lxxx, 1908), in which the
histological results are compared with the results of stimula-
tion experiments performed on the lemur's brain by Prof.
Halliburton, and a paper of a similar nature, but dealing with
the brain of the marmoset, has been produced by Mott,
Halliburton, and the present author (Mott, Schuster, and
Halliburton, "Cortical Lamination and Localisation in the
Brain of the Marmoset," 'Proceedings of the Royal Society,'
B., vol. lxxxii, 1910).

MATERIAL AND METHODS.

The material used in the present paper consisted of the
brain of a specimen of Papio hamadryas which had died
in the gardens of the Zoological Society.

Each hemisphere was cut into a number of blocks (seventy
or more), arranged in such a way as best to secure that as
much as possible of the cortex was cut in planes at right
angles to its surface, since in oblique sections the nature of
the cell lamination is almost impossible to determine. The

outlines of the blocks were carefully plotted in drawings of the brain. From each block sections $10\,\mu$ thick were taken and stained with polychrome methylene-blue. As no satisfactory sections of the insula were obtained, the cortex in this part of the brain has not been described.

In the investigation of these sections the admirable works of Brodmann[1] on Cercopithecus and Campbell[2] on the chimpanzee and orang-outang were of great assistance to me, and as far as possible my observations have been brought into line with theirs.

My observations differ from Brodmann's in that I have not described so many types of cortex. This is due to a difference in judgment and not to antagonism with regard to matters of fact. Since in the area covered by each main type local differences are present, and since the main types in many cases shade into one another, it would be possible to describe many more varieties of structure than are mentioned by Brodmann. One must arbitrarily fix a limit to the number of types distinguished, and I have fixed mine at a smaller number than he.

For illustrating the structures described in the text, outline drawings of the cells were made under the Abbé Zeichenapparat, and these were afterwards blacked in with ink so that the cells are represented in silhouette.

It was thought advisable to prefix a short description of the fissures to the principal part of the paper.

FISSURES IN THE BRAIN OF PAPIO HAMADRYAS.

The Sylvian fissure (FS.) and sulcus centralis (c.) call for no special comment. Anterior to the latter the following fissures are present :

[1] K. Brodmann, " Beitrage zur histologischen Lokalisation der Grossheikrinde Dritte Mitheilung; Die Rindenfelder der Niederen Affen," ' Journ. für psych. u. Neurol.,' Bd. iv, Heft 5/6, 1905.

[2] A. W. Campbell, ' Histological Studies in the Localisation of Cerebral Function,' Cambridge, 1905.

Sulcus arcuatus (*arc*.).—From the most posterior portion of the backwardly directed convexity of this fissure a straight branch runs upwards and backwards. The upper limb in the right hemisphere is united at its extremity with one of the sulci of the frontalis superior series. The lower limb in both hemispheres runs straight downwards and forwards, and ends about a centimetre above the anterior end of the Sylvian fissure.

Sulcus inferior transversus (*it*.) runs obliquely upwards and forwards between the lower ends of the sulcus centralis and sulcus arcuatus; in the right hemisphere it is connected with the Sylvian fissure.

Sulcus rectus (*rect*.) runs horizontally forwards from a position about 5 mm. in front of the sulcus arcuatus, to end about the same distance from the frontal pole. Between its posterior end and the lower portion of the sulcus arcuatus lies the sulcus diagonalis (*d*.), a shallow oblique fissure better marked in the right hemisphere than in the left.

The sulcus præcentralis superior and sulcus frontalis superior (*fs. 1, 2, 3, 4*) are together represented by a series of shallow fissures, of which the posterior (*fs.$_1$*) is the best developed. This lies in a more or less sagittal direction, while the other members of the series are more transversely placed.

On the orbital surface is found a sulcus orbitalis (*orb*.) lying near the mesial border; this is triradiate in the right hemisphere, but a simple, more or less sagittal, fissure in the left. On the lateral side of this is the obliquely placed sulcus fronto-orbitalis (*fo*.), the anterior outer end of which just reaches the lateral surface of the hemisphere. This fissure is quite well defined, though not more than three or four millimetres deep. Its shape is complicated in the left hemisphere by the presence of a shallow forwardly directed bifurcated branch.

The sulcus temporalis superior (*Ts*.) is a long, well-developed fissure extending both in front of and behind the Sylvian fissure. Its posterior end is bifurcated in the right

hemisphere but not in the left. Below it, in the temporal lobe, lie one or two shallow grooves ($Tm._{1, 2}$, etc.), which may be taken to represent the sulcus temporalis medius.

The sulcus post-centralis superior (*pcs.*) is a shallow groove lying almost horizontally opposite the upturned posterior end of the sulcus cinguli.

The sulcus intra-parietalis (*ip.*) starts anteriorly in the space which is bounded above and in front by the sulcus centralis, and below and behind by the Sylvian fissure. It runs at first upwards and backwards, then turning backwards, disappears underneath the occipital operculum. Here it bifurcates. Its outer branch runs outwards on the anterior wall of the sulcus lunatus, and then divides into two rami, of which one runs to the bottom of that fissure while the other runs upwards. The inner branch, by far the larger of the two, is called the ramus parieto-occipitalis (*rpo.*) of the sulcus intra-parietalis. It cuts very deeply through the supero-mesial border of the hemisphere, then runs straight downwards to end in a bifurcation, the branches of which lie more or less parallel to the sulcus calcarinus.

Owing to the extent of the occipital operculum, this ramus parieto-occipitalis appears to be a mesial continuation of the sulcus lunatus; in reality the two fissures are partially separated by a submerged gyrus lying near the supero-mesial border.

The fissura parieto-occipitalis (*fpo.*) is a triradiate fissure, the two posterior rays of which arch round the anterior limb of the terminal bifurcation of the parieto-occipital branch of the sulcus intra-parietalis. These two rays are better developed in the left hemisphere than in the right, and there the lower one forms a superficial connection with the posterior limb of *rpo.* The anterior ray is poorly developed.

The sulcus subparietalis (*sp.*) (posterior limbic sulcus) lies between the fissura parieto-occipitalis (*fpo.*) and the sulcus cinguli. The main portion of this fissure runs upwards and slightly backwards; its lower end is divided into two

branches, which are better marked in the left hemisphere than in the right.

The sulcus cinguli (*Sc.*) (intercalary or calloso-marginal fissure) is quite typical in its arrangement. At its anterior end lie two shallow sulci rostrales (*ro.*), with the upper of which it is, in the right hemisphere, in connection.

The sulcus collateralis (*Col.*) is in the right hemisphere divided into three segments ; the most anterior of these (*col.*$_1$) lies obliquely between the sulcus rhinalis and the anterior end of the sulcus temporalis superior. The middle segment (*col.*$_2$) is the longest; it runs sagitally backward. Between its posterior portion and the sulcus calcarinus lies the third segment (*col.*$_3$), the main portion of which runs parallel to that fissure, to end posteriorly in a transverse member. In the left hemisphere only two segments are present, the anterior (*col.*$_1$) corresponding exactly to the anterior segment in the right hemisphere, while the posterior segment of the left hemisphere corresponds to the two posterior segments of the right ; at its hinder end it runs upwards and ends very close to the sulcus calcarinus.

In the left hemisphere a shallow ⊤-shaped sulcus (*T.*) is present lying between the posterior part of the sulcus collateralis and the sulcus calcarinus.

The sulcus rhinalis (*rh.*) is quite typical.

The sulcus lunatus (*lun.*) ("Affenspalte") is well developed in both hemispheres ; its posterior lip is produced forwards to form an operculum. Curving round its lower end is the deep sulcus occipitalis inferior.

The sulcus occipitalis inferior (*Oi.*), the upper lip of which is produced downwards to form a well-marked operculum. Behind this fissure, curving round the tentorio-lateral margin, is another sulcus, which is independent in the right hemisphere, but connected with it in the left.

The sulcus occipitalis lateralis (*Ol.*) lies horizontally between the sulcus lunatus and the occipital pole. It is a very deep fissure, which cuts obliquely downwards into the hemisphere so that its lower lip forms an operculum. Its

anterior end is bifurcated in the right hemisphere. One or two shallow grooves lie between this and the sulcus occipitalis inferior.

The sulcus calcarinus (*cal.*) at its anterior end joins the fissura hippocampi ; it runs a sigmoid course backwards, to end in a long bifurcation near the occipital pole. The upper branch is by far the longest, and its upper end just reaches the lateral surface of the hemisphere. In the right hemisphere it gives off a short downward branch.

FRONTAL LOBE.

Precentral (Motor) Type (fig. 1).

This type of cortex is characterised by its great depth, which reaches to over 2·7 mm., the presence of the Betz cells, and the absence of a distinct layer of " granules." The drawing (fig. 1) is taken from the lateral surface of the hemisphere a short way in front of the upper end of the sulcus centralis. Here the breadth of the cortex is about 2·7 mm., but only the upper 2·4 mm. are drawn. The Betz cells occupy a broad zone, otherwise rather poor in cells, which stretches from 1·3–1·9 mm. from the surface. They appear to be larger here than in other parts of the precentral area. The cell bodies of the largest are about 70μ in length by 50μ in breadth, but the massive processes given off from the apex and base render accurate measurements impossible, since it is difficult to say where the cell-body ends and the bases of the apical process or other dendrites begin. These cells are slightly smaller on the mesial surface, and gradually diminish in size as one passes downwards over the lateral surface towards the Sylvian fissure. About halfway down they measure only $50 \times 30 \mu$.

The other cell layers are as follows :

(i) The lamina zonalis is about 1 mm. broad.

(ii) Lamina granularis externa reaches to a depth of about ·3 mm. Its constituent cells are small pyramids and granules ; these vary in size in different regions, and appear to be rather larger on the mesial than on the lateral surface. The largest of the small pyramids are about $15 \times 12 \mu$.

(iii) Lamina pyramidalis is about 1 mm. broad, extending from a depth of ·3 to a depth of 1·3 mm.; as is usual, the cells increase in size from above downwards. The largest cells in the area figured are about 35μ in length $\times 20 \mu$ in breadth ; but this particular strip of cortex, though exceptionally rich in large Betz cells, is rather poorer than others in large pyramids of layer iii.

(iv) Lamina granularis interna is represented by a few scattered granules in the lower part of layer iii and upper part of layer v.

(v) Lamina ganglionaris. The Betz cells have already been described ; the other cells contained in the layer resemble either those of layer iii or of layer vi.

(vi) Lamina multiformis is rather poor in cells. These are arranged in regular radial rows, and many of them have strong, downwardly directed processes.

Anterior Precentral Type (fig. 2).
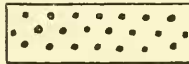
The whole depth of the cortex is about 2·2 mm.; it is built up as follows :

(i) Lamina zonalis, breadth just over ·1 mm.

(ii) Lamina granularis externa, breadth about ·2 mm. This is composed of small pyramids and granule cells, the former measuring $10–15 \mu$ in length by $9–12 \mu$ in breadth, and the latter being some $9–12 \mu$ in diameter.

(iii) (iv) and (v) Lamina pyramidalis, lamina granularis interna, lamina ganglionaris are not very clearly separated ; a

narrow strip, such as is figured, hardly shows any lamination, but if a wide area of cortex is examined under the low power of the microscope one can distinguish (1) an upper zone (iii a) consisting mostly of medium-sized pyramids, which stretches downwards to a depth of about ·8 mm. (2) A tendency to form a definite layer of large pyramids (iii b) at a depth of ·9–1·2 mm. from the surface. The size of these cells may be 30–50 μ in length by 20–25 μ in breadth. (3) A stratum, rather poor in cells, extending from 1·2–1·4 mm. (4) Another, but less well-defined, layer of large pyramidal cells (v) at 1·4–1·6 mm. These cells are in some places rather larger than those at iii b, in other places about the same size or rather smaller ; they are in all places much less numerous. A few granule cells and small triangular and irregular-shaped cells are present between, and interspersed with, both the upper and lower layers of large pyramids.

(vi) Lamina multiformis occupies the rest of the cortex ; it contains cells of varied shapes, the most prevalent being roughly triangular cells with long processes extending both upwards and downwards.

Extent and Boundaries.—The precentral cortex on the mesial surface is bounded below by the sulcus cinguli ; on the lateral surface it extends posteriorly to the bottom of the sulcus centralis; below it falls considerably short of the Sylvian fissure. Along its free anterior and lower border it passes gradually into the anterior precentral type.

The anterior precentral type is also bounded below on the mesial surface by the sulcus cinguli; along the supero-mesial border it extends to more than half the distance between the upper end of the sulcus centralis and the frontal pole. Its upper anterior extension forms a broad band on the lateral surface, the posterior part of which is bounded below by the horizontal limb of the sulcus arcuatus. The vertical portion of that fissure serves as the anterior boundary of the narrow strip of this cortex, which lies in front of the lower portion of the precentral area. Approaching the Sylvian fissure the anterior precentral type alters considerably in character ; the large

pyramids, both supra- and sub-granular, become smaller and more densely packed together, and the lamina granularis interna is more easily recognisable. In this condition the cortex is prolonged forward beyond the lower end of the sulcus arcuatus, where it passes gradually, on the one hand, into the frontal, and, on the other, into the posterior orbital type. In structure this lower forward extension of the anterior precentral bears a marked resemblance to the anterior part of the posterior orbital cortex. In position it has some points in common with Brodmann's type 10, which it resembles in having a layer of granules distinguishable but not well developed.

Posterior orbital type (fig. 5).
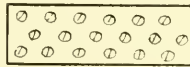
The position of the particular strip of cortex shown in fig. 5 was near to the posterior border of the orbital surface just lateral to the sulcus orbitalis. The cortex is here 1·8 mm. in depth. The lamina zonalis extends to a depth of ·25 mm., and is succeeded by a very poorly developed lamina granularis externa; this in turn gives place to the lamina pyramidalis. The lower and larger pyramids of the latter form together with the cells of the lamina ganglionaris a zone rich in cells of moderate size, which extends from a depth of ·7 mm. to a depth of 1·3 mm. A faint indication of the lamina granularis interna lying at a distance of about ·9 mm. from the surface suggests that only the upper border of this zone should be reckoned to the lamina pyramidalis, and that the greater part of it is derived from the lamina ganglionaris. The lower half millimetre of the cortex is occupied by the lamina multiformis, the greater proportion of the cells of which are of a broad pyramidal form with basal processes extending horizontally. These cells tend to be arranged in horizontal rows, separated by tangentially running bundles

of fibres, a type of arrangement which, though obvious even in a narrow strip like that figured, becomes very conspicuous when a considerable width of cortex is examined under a low power.

The posterior orbital type is of practically identical structure with Brodmann's type 11, but it shows some differences in its extent and boundaries.

According to Brodmann, this type covers the greater part of the orbital surface in the hemisphere of Cercopithecus, being absent only from its anterior portion and the gyrus rectus. In Papio a type of cell-lamination exactly answering to the description given above is found only in the posterior quarter of this part of the hemisphere, and there it extends across the gyrus rectus, and is in continuity with the anterior limbic type over the orbito-mesial border. In front it extends further forward along the lateral than along the mesial border, but it gradually changes its character; the internal layer of granules becomes more marked, and the tangential arrangement of the lamina multiformis less marked, till finally, at about the position indicated in the figure, it is definitely replaced by frontal or prefrontal cortex, though where the exact boundary may be it is impossible to say owing to the gradual nature of the transition.

The intermediate precentral area of Campbell is of approximately the same structure and extent both in man and in the higher apes (orang and chimpanzee). In structure it resembles the precentral (motor) cortex in almost all points, except that no giant Betz cells are present in the internal layer of large pyramidal cells. The elements of this layer are smaller and less numerous than those of the outer layer of large pyramids. Between the two layers is a stratum poor in cells, which occupies the position of the layer of stellate (granule) cells present in most other regions. This type of cortex extends from the mesial surface, over the supero-mesial border, then downwards and outwards over the lateral surface, and ends by occupying a considerable area of the orbital face of the hemisphere. On the mesial surface it

is bounded behind by the precentral area, below by the calloso-marginal fissure, and extends forward for a considerable distance. Its anterior boundary crosses the superomesial border about 2 cm. in front of the precentral area in the chimpanzee, and somewhat further forward in the orang. On the lateral surface it forms a zone lying in front of the precentral area, which is broad above, but becomes narrower lower down, being bounded in front for a short distance by the sulcus arcuatus.

As it nears the Sylvian fissure it extends forwards over the lower portion of the sulcus arcuatus and occupies a more or less rectangular area bounded above by the sulcus rectus and below by the superior limiting sulcus of the island of Reil— the part of the hemisphere which, according to Campbell, corresponds to the pars basilaris of the human brain. In front it invests the upper end of the sulcus fronto-orbitalis, "then turning abruptly downwards, and still following the fronto-orbital sulcus, it coats the convolution forming its anterior wall and is finally arrested well down on the inferior (orbital) surface by the sulcus orbitalis."

In Brodmann's description of the brain of Cercopithecus the area which corresponds to Campbell's intermediate precentral is occupied by three types of cortex. Type 6, which agrees in structure with the intermediate precentral, has approximately the same extent on the mesial surface and on the upper and middle portions of the lateral surface, but it never extends far beyond the sulcus arcuatus, which lies along its whole length just behind the anterior boundary. The region roughly corresponding to the pars basilaris is occupied by type 10, which in the orbital surface gives place to type 11.

Type 11 resembles type 6 in the absence of a layer of granules but differs from it in the following points : (1) The external and internal layers of large pyramids (Brodmann's layers iii b and v) are fused to form a clearly delimited band, the cortex is narrower, and to judge from the photographs the cells are considerably smaller.

In Type 10 the granule layer is present but poorly developed. Types 10 and 11 agree in a point which Brodmann regards as important, namely, that owing to the tangential arrangement of the fibres in the lower part of the cortex the cells of the innermost layer tend to lie in tangential rows and not in radiating rows more or less vertical to the surface.

The Frontal and Prefrontal Types (figs. 3 and 4).

The drawing of the frontal cortex (fig. 3) is taken from the lateral surface of the hemisphere on the upper side of the sulcus rectus, about two thirds of its length from its posterior end. Here the depth of the cortex is approximately 2 mm. The lamina zonalis (i) occupies the upper ·2 mm. of this. The lamina granularis externa (ii) extends to a depth of rather over ·3 mm., while the lamina pyramidalis (iii) forms a zone of which the lower border lies ·9 mm. from the surface.

There is nothing remarkable about any of these layers; as is usually the case the pyramids of layer iii increases in size from above downwards, but the large cells near the lower border do not form at all a well-marked layer. The lamina granularis interna (iv) extends from a depth of ·9 to a depth of 1·2 mm. or lower, but it is overlapped by the lamina ganglionaris (v), the large cells of which spread upwards among the granules and downward to a depth of about 1·4 mm. The rest of the cortex is occupied by the lamina multiformis (vi), which fades away into the white matter. The cells of this layer are more concentrated near its upper border, thus forming a distinct band between which and (v) is a slightly clearer stratum. This type of cortex corresponds exactly with Brodmann's type 9 or Campbell's " frontal."

The prefrontal type is illustrated in fig. 4—a drawing of a strip of cortex taken from the gyrus rectus about half-way along it.

The prefrontal type differs from the frontal in its comparative poverty in cells and in the smaller size of the cells of layers iii b and v, particularly the former. Its depth is also less. Measurements of the cells in the two layers mentioned were made near the posterior boundary of the frontal region and in the prefrontal. It was found that in the former position the largest cells at iii b were about 40μ in length $\times$ 30μ in breadth, while in the latter $30 \mu \times 23 \mu$ represents approximately their dimensions. The general average is, however, in each case much less. The corresponding figures for layer v are : in posterior part of the frontal area about the same as for layer iii b, while in the prefrontal area, $35 \mu \times$ 27μ roughly indicates their size. In fig. 3, which is taken fairly far forward in the frontal region, it will be noticed that the subgranular pyramids are rather larger than those situated above the granules, and that the cells of each layer are slightly larger than the corresponding cells in fig. 4.

The extent of the lamina multiformis and the shape of its cells depend to a great extent to the prevalent direction of the fibres of the underlying white matter; where this is tangential the layer is shallow and its cells tend to be drawn out tangentially ; where the fibres radiate upwards towards the surface the cells are elongated along an axis vertical to the surface, and the layer tends to be deep. This effect of the direction of the fibres is not always confined to the lamina multiformis, but the layers lying above it may all be involved. It is not confined to one part of the hemisphere, but may be noted in all. It is mentioned here because, in the part of the prefrontal region figured, the fibres are arranged tangentially, while in fig. 3 they are radial in direction. It seemed desirable to explain that this difference is not an essential difference between the two types. In the region of the frontal pole the direction of the fibres of the prefrontal cortex is radial, and the result is a marked difference of appearance in the shape and arrangement of the cells, particularly of the lower layers. The condition described by Brodmann as type 12 may thus be distinguished : "slender pyramids," "layer vi much

extended and passing gradually into the white matter through isolated, scattered spindle-cells."

Extent of Frontal and Prefrontal Types.—The extent and boundaries of the frontal and prefrontal types are shown in the figures, and hardly call for verbal description. The limits are in most places vague and indefinite, but an exception to this statement must be made in the case of the sulcus arcuatus, which forms the posterior, and, to a certain extent the upper boundary of the frontal area on the lateral surface. On the anterior wall of that fissure the cortex is intermediate in character between the frontal and anterior precentral types.

The granule layer is slightly less accentuated than in the former, while a few very well developed pyramidal cells, lying some above it and some below it, are distinctly suggestive of the latter type. This intermediate strip corresponds to Brodmann's type 8. A difference will be noted in the region between Papio and Cercopithecus, namely, that in the latter the anterior precentral cortex extends in front of the sulcus arcuatus and the intermediate type 8 lies well in the surface; in the former the anterior precentral type stops at the bottom of the fissure.

The whole of the frontal lobe in the chimpanzee and the orang lying in front of the intermediate precentral and limbic areas is covered by the frontal and prefrontal types of cortex. These agree in the possession of a distinct layer of granules, which is broad and well-defined, but not so densely crowded with cells as the corresponding stratum of the parietal or temporal areas. Above and below there is in each case a layer of large pyramids. The chief point of difference lies in the smaller size, slenderer forms, and reduced numbers of the constituent elements of these two layers in the prefrontal area. There is no well-marked line of demarcation, but the large pyramids, which are best developed near the posterior border of the frontal area, gradually undergo reduction in size and number.

Brodmann's description of the corresponding region in the

hemisphere of Cercopithecus agrees in the main very well
with Campbell's account summarised above. The slight
differences to be noted may be due to the gradual nature of
the transition between one type of cortex and its neighbours.
Thus Brodmann recognises four different types against
Campbell's two, namely, Nos. 8, 9, 12, and 25. Of these,
No. 9 clearly corresponds with Campbell's frontal type, and
No. 12 with the prefrontal, though the extent of the area
occupied by No. 12 is relatively considerably less.

No. 8 lies immediately in front of the sulcus arcuatus; it
occupies a narrow strip of the lateral surface of the hemi-
sphere, bounded behind by type No. 6 and in front by type
No. 9. In structure it resembles the posterior portion of
Campbell's frontal area, being intermediate between the two
types, which it separates. No. 25 lies completely on the
mesial surface, where it occupies a comma-shaped area between
No. 9 (frontal area) and No. 24 (the anterior limbic area).
Its structure is intermediate between these.

Parietal Occipital and Temporal Lobes.

Post-central Type (fig. 6).
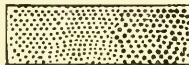
The post-central type of cortex is illustrated in fig. 6,
which is taken from the crown of the post-central gyrus a
little way below the anterior end of the sulcus post-centralis
superior (pcs.). The cortex is here 1·7 mm. in depth, of which
the lamina zonalis (i) occupies the upper ·1 mm. The lamina
granularis externa (ii), composed as usual of small pyramids
and granules, is fairly well developed, but not so closely
crowded with cells as to be sharply marked off from the under-
lying lamina pyramidalis; it reaches to a depth of about
·25 mm. The lamina pyramidalis (iii) is very distinctly sub-
divided into an upper stratum (iii a) containing medium-sized

pyramids in no wise remarkable, and a lower stratum (iii b), which is very conspicuous, and constitutes the most characteristic feature of the post-central cortex. iii b extends from a depth of ·5 mm. to a depth of ·85 mm., and its principal constituents are large cells closely crowded together, and lying about three deep. Their shape and approximate size may be gathered from the drawing; they are elongated pear-shaped or pyramidal cells drawn out above into a broad process which takes the stain rather faintly. It is difficult to give a numerical indication of their size, but this may be as much as 60 or $70 \mu \times 30 \mu$. The lamina granularis interna is a dense layer of granules intermixed with small pyramids; its lower limit is ·1 mm. below that of iii b, but above it is extended by columns of small cells which lie between the large elements of that lamina.

Closely underlying iv is the lamina ganglionaris v. This consists of a number of triangular quadrilateral and other elements of comparatively small size, among which are scattered occasional pyramids of notably superior size; these cells, which lie near the lower border of the layer, at a depth of 1·2 mm., are inferior in size to the supra-granular pyramids, and differ from them also in shape; their cell-bodies are more slender, and their apical processes narrower and more darkly staining. The rest of the cortex is occupied by the lamina multiformis (vi), which is separated from v by a zone comparatively poor in cells. It cannot be subdivided into a lamina triangularis and a lamina fusiformis.

The cortex described above corresponds to Brodmann's types Nos. 1 and 2. As it dips over in front into the sulcus centralis it alters somewhat in character; the whole cortex becomes narrower; the large cells at iii b become reduced in size and number; the layer of granules (iv) grows less distinct, and the lamina ganglionaris suffers the same changes as iii b.

According to Brodmann, the large cells at iii b and v, which form the most characteristic feature of the post-central cortex, are larger and more numerous near the posterior lip

of the gyrus centralis posterior than at the summit of the
gyrus. He thus distinguishes two types—No. 1 clothing the
summit of the gyrus, and No. 2 its posterior lip. I do not
find that this is the case in Papio. Here the post-central
type is at its best in the middle portion of the gyrus, becomes
less well-developed near the posterior border, and as it passes
downwards into the intra-parietal fissure it loses its distinctive
features as it changes into the neighbouring type. A gradual
reduction of the size and numbers of these large cells, par-
ticularly those of the lamina ganglionaris, can also be
observed as one passes downwards over the lateral surface ;
they are largest and numerous in the upper half of the gyrus,
and become very much less conspicuous near the lower end
of the sulcus centralis. On the mesial surface the large cells
of the lamina ganglionaris are particularly well represented,
while those of the lamina pyramidalis inferior are neither so
large nor so numerous.

Extent of the Post-central Type.—The post-central
cortex, modified locally as described above, occupies on the
mesial surface the posterior portion of the para-central lobule.
On the lateral surface it extends anteriorly to the bottom of
the sulcus centralis, and occupies the greater part of the
gyrus centralis posterior. Above, where the sulcus intra-
parietalis bends backwards, it passes into the superior parietal
type, while below it extends in front of the lower end of the
sulcus centralis, and becomes continuous anteriorly with the
lower portion of the anterior precentral, while posteriorly it
changes into the inferior parietal cortex.

Superior Parietal Type (fig. 7).
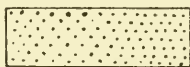
The superior parietal type is illustrated in fig. 7. The
general plan of its layers and their relative extent is very
much the same as that of the post-central type. The most

striking difference is to be found in the lamina pyramidalis inferior (iii b). Here, though numerous large pyramids are present forming a fairly definite layer, they are notably inferior in size to those of the post-central type, while in number also they are conspicuously less. They are confined to a narrow zone lying immediately above the granules, while in the post-central cortex they form a broad stratum which occupies more than half of the whole lamina pyramidalis.

Extent and Boundaries.—The superior parietal cortex occupies on the lateral surface the greater part of the area bounded laterally by the sulcus intra-parietalis, mesially by the border of the hemisphere, posteriorly by the upper part of the sulcus lunatus, and anteriorly by the post-central cortex. It extends also on to the mesial surface, where it lies between the sulcus cinguli and the ascending limb of the sulcus subparietalis. Below it passes into the posterior limbic type, and behind into the inferior parietal.

Inferior Parietal Type (fig. 8).

The inferior parietal cortex is illustrated in fig. 8, which is taken from the lateral surface of the hemisphere just posterior to the sulcus intra-parietalis at a level a little below the posterior end of the sulcus temporalis superior. The cortex is here 1·9 mm. deep. The lamina granularis interna (iv) is very well marked; it is about ·2 mm. in breadth, its upper margin lying at a depth of ·8 mm. Above it lies a zone of large pyramids (iii b) of approximately the same breadth. The cells contained in it are smaller than their homologues in the superior parietal cortex. In shape they are rather slender : their length may be as much as $40\,\mu$, but their breadth is never much over $20\,\mu$.

Below the granules is a fairly well-developed lamina ganglionaris (v). The majority of the cells in this layer are

much smaller than those at iii b, but scattered among them are a few of outstanding size, yet not so large as the corresponding cells of the post-central or superior parietal regions. The lamina multiformis may be divided into an upper lamina triangularis and a lower lamina fusiformis. The cells of the former are large and numerous with broad triangular or quadrilateral forms predominating, while those of the latter are smaller and slenderer, and many of them approach the fusiform in shape. On the mesial surface the breadth of the cortex is about $\frac{1}{5}$ mm. less. In this reduction, which is associated with the more tangential arrangement of the fibres in the underlying white matter, the lamina multiformis is alone much affected. Not only is this layer reduced in breadth, but its constituent cells are reduced in size and numbers.

This type of cortex bears a considerable resemblance to the temporal and some to the frontal cortex. It differs from the latter, however, in many important points. It is of about the same breadth but much richer in cells. The lamina zonalis is narrower, the lamina granularis externa more clearly defined. The large pyramids at iii b are much more numerous and form a more distinct layer. The lamina granularis interna is also much richer in cells, and more obviously separated from the adjacent strata. The lamina ganglionaris is not so well developed, but the lamina multiformis is broader and richer in cells, and does not show the gradual transition to the white matter which Brodmann observes is a characteristic of the frontal lobe.

Extent and Boundaries.—The inferior parietal cortex lies behind and below the superior parietal both on the lateral and on the mesial surface. On the mesial surface it covers a broad area bounded in front by the sulcus subparietalis and behind by the ramus parieto-occipitalis of the intra-parietal fissure. Below it passes gradually into the posterior limbic and occipital types. Above it passes over the supero-mesial border and forms a narrow strip between the superior parietal area and the upper end of the sulcus lunatus, then crosses the sulcus

intra-parietalis, and invests the triangular area lying between
that fissure and the upper end of the sulcus temporalis
superior; below this it extends forwards and downwards on
the upper side of the Sylvian fissure; it gradually becomes
narrower, and finally dies away a little in front of the lower
end of the sulcus centralis.

The inferior parietal cortex corresponds in position and
structure to Brodmann's type 7. That part of it which lies
in the mesial surface and on the lateral surface above the
intra-parietal corresponds with Campbell's parietal area, but
is notably less in extent than in the higher apes or in man.
The remaining area is according to Campbell clothed with
temporal cortex, but there is so great a similarity between
the two types that there is no great antagonism in the two
descriptions.

Calcarine Type (fig. 9).

The calcarine type of cortex is illustrated in fig. 9, a draw-
ing taken from the wall of the lower branch of the posterior
bifurcation of the calcarine fissure. Here the cortex is just
over 1·5 mm. in breadth.

The lamina zonalis occupies rather more than the upper
·1 mm. of this, and the lamina granularis externa forms a
narrow border of small pyramids and granules below it. The
lamina pyramidalis, consisting of small- and medium-sized
pyramids, extends to a depth of ·4 mm. It is densely crowded
with cells, which follow the usual arrangement in being larger
near the lower border. The largest of them do not appear to
exceed a length of 25 μ. What is considered by Brodmann to
be homologous with the lamina granularis interna occupies
about half the total breadth of the cortex, extending, as it
does, from a depth of ·4 to a depth of 1·15 mm. It can be
divided into three strata : (1) An upper layer of granules

interspersed with a few small pyramidal cells; this extends
from ·4–·55 mm. (2) A middle layer, ·25 mm. wide, corre-
sponding to Campbell's layer of large stellate cells. This is
rather poorer in cells than the rest of the cortex, being the
region occupied by the stria of Gennari. A considerable
number of cells are, however, present, and these seem to be
concentrated rather nearer to the upper than to the lower
border. The most conspicuous are the large stellate cells
themselves, the length and breadth of which may be about
25 μ. The majority of these seem to be in the form of rather
broad pyramids, sending out an apical process and horizontal
basal processes. Scattered among them are granules and
smaller pyramids. (3) The lower layer of granules extends
from a depth of ·8 to a depth of 1·15 mm. This can be clearly
subdivided again into an upper layer of large pyramidal and
irregular-shaped cells and a lower layer consisting almost
entirely of small granules. The lamina ganglionaris is com-
paratively poor in cells, and the cells themselves are small.
The solitary cells of Meynert, which are reckoned to belong
to this layer, are actually sunk within the upper part of the
underlying lamina multiformis; they are not very numerous,
and only one of them is shown in the drawing; in size they
may be about 30 μ in length by about the same breadth.
The lamina multiformis is very narrow, but richer in cells
than the layer above it; the cells themselves are small.

Extent and Boundaries.—The calcarine cortex is on
the mesial surface largely confined to the calcarine fissure; at
the posterior bifurcation of the latter it emerges on to the
surface and covers the whole area lying behind it. Spreading
on to the lateral face of the hemisphere it occupies the greater
part of the large area, bounded in front by the sulcus lunatus,
to the lip of which it almost extends. It covers the walls of
the lateral occipital fissure. Near the occipital pole it does
not extend much below that sulcus, but in front it spreads
downwards much farther, yet always falls far short of the
sulcus occipitalis inferior.

Occipital Type (fig. 10).

The occipital type is illustrated in fig. 10, which is drawn from the lateral surface of the hemisphere between the sulcus lunatus and the upturned end of the sulcus temporalis superior. The cortex is here 1·6 mm. deep, of which the lamina zonalis occupies rather over ·1 mm. The lamina granularis externa is not clearly separated from the subjacent lamina pyramidalis. The latter extends downwards to a depth of ·75 mm., and its lower half is characterised by the presence of a number of elongated pyramids, which reach a length of 50 μ and more. The lamina granularis interna is narrow but very well marked; the granules are arranged closely together, and very few cells of other forms are present among them except in so far as they themselves extend upwards among the bases of the large pyramids. The lower border of this layer lies at a depth of ·9 mm. The lamina ganglionaris is composed of rather small pyramids; it is poor in cells and appears as a clear band under the low power of the microscope. It is the conspicuous presence of a layer of large pyramids above the granules, coupled with their conspicuous absence below, which gives the distinctive character to this type of cortex. The lamina multiformis is well developed and about ·4 mm. broad. Along its upper border the elements are larger and more triangular, while near its lower edge they are smaller and more fusiform.

The occipital type, which corresponds to Campbell's visuo-psychic and Brodmann's types 18 and 19, is not of uniform structure over the whole area which it invests. Immediately adjacent to the calcarine area, which it completely surrounds, it is much narrower than in the position selected for illustration, fewer cells are present, and the lamina ganglionaris is relatively clearer. As it approaches the temporal .or inferior parietal areas which form the greater part of its anterior boundary it assumes more the character of those

types. It is this intermediate structure which forms Brod-
mann's type 19.

Extent and Boundaries.—The occipital type completely
surrounds the calcarine, the boundary between the one type
and the other being quite abrupt and definite. Very different
is the transition between the occipital and the inferior parietal
temporal and posterior limbic types, into which it passes
anteriorly. This is so gradual that it is almost impossible to
say where the one ends and the other begins, and the boun-
dary is in consequence very difficult to describe. Under
these circumstances I do not attempt a verbal description,
but merely refer to the figures A, B, C, D.

Temporal Type (fig. 11).
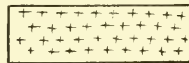
The essential features of the cortex covering the greater
part of the temporal lobe are shown in fig. 11, which is taken
from the middle temporal gyrus in its posterior half. Its
depth is here about 2 mm.

The lamina zonalis extends to a depth of ·2 mm. The
lamina granularis externa is closely packed with cells and
fairly well separated from the underlying lamina pyramidalis.
The latter extends to a depth of rather more than half the
whole thickness of the cortex. The large pyramids (iii b),
which reach a length of 30 μ or more, form a broad zone near
the inner border of the layer.

The lamina granularis interna is exceptionally well
developed, and stretches from 1·1 mm. to 1·3 mm. from the
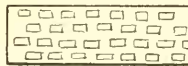surface.

Beneath this layer the development of the cortex is poor in
comparison with the parts above, but the lamina ganglionaris
is fairly well developed, though its cells are slightly smaller
than those at iii b. A slightly clearer space separates it from
the lamina multiformis.

The description given above applies in its details only to the middle temporal gyrus. The cortex of the superior temporal gyrus differs in many respects. It is broader and poorer in cells. The lamina granularis interna is not so well developed. The lamina ganglionaris is, on the whole, not so clear, but contains a few large cells scattered through it.

A change in structure is also apparent as one moves round the temporal lobe in the other direction. As one approaches the hippocampal gyrus the cortex becomes narrower, and the layer of granules less well developed.

The extent of the olfactory cortex is shown in fig. c, but it has not been thought necessary to give a special description or drawing of its structure.

Anterior Limbic Cortex (fig. 12).

The anterior limbic type is illustrated in fig. 12, which is taken from the mesial surface of the hemisphere just above the anterior portion of the corpus callosum. The cortex here reaches a depth of 1·9 mm. Its chief characteristic is the absence of any very definite system of stratification. The lamina granularis externa is very poorly developed; it passes gradually into the lamina zonalis above it and is hardly possible to separate from the lamina pyramidalis below. The latter is somewhat sparsely populated with small and medium-sized pyramids until a depth of ·6 or ·7 mm. is reached; below this, extending for about half a millimetre, is a zone of cells considerably larger in size and more closely arranged, which probably represents the lower part of the lamina pyramidalis (iii b) and the lamina ganglionaris (v). There is no trace of the lamina granularis interna. The lamina multiformis is also poor in cells, of which the upper ones are of fair size and triangular form, while the lower ones are smaller and more spindle-shaped.

Posterior Limbic Cortex (fig. 13).
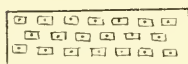
The posterior limbic cortex is illustrated in fig. 13, which is taken from the mesial surface of the hemisphere just above the posterior end of the corpus callosum. It differs from the anterior limbic type in (1) a greater richness of cells, (2) the better development of the lamina granularis externa, (3) the presence of a lamina granularis interna. The latter, though clearly defined, is not so well developed as in the inferior parietal or occipital types, which it resembles in some respects. The lamina ganglionaris follows closely below the internal layer of granules. It is well developed, the cells on the whole being larger and more numerous than in the strip actually drawn.

Extent and Boundaries.—The anterior limbic cortex lies between the sulcus cinguli and the corpus callosum ; it is continued forward as a broad band round the anterior end of the latter. This anterior portion is separated from the frontal cortex by an area intermediate in character. Posteriorly it extends a little way behind the region of the mesial surface, in which the anterior precentral changes into the precentral type. At this point, by the gradual acquisition of an internal layer of granules, it becomes transformed into the posterior limbic type. The latter extends round the posterior end of the corpus callosum, changing gradually above and behind into the types of cortex on which it abuts.

The posterior limbic coxtex corresponds to Brodmann's type 23, the anterior to his type 24, while the area intermediate in character between the limbic and the frontal is equivalent to his type 25.

EXPLANATION OF PLATES 24–30,

Illustrating Mr. E. H. J. Schuster's paper, "Cortical Cell Lamination of the Hemispheres of Papio Hamadryas."

PLATE 24.

The two hemispheres seen from different points of view to show fissures and distribution of various types of cortex.

Fig. A.—Dorsal view of both hemispheres.

Fig. B.—Ventral view of both hemispheres.

Fig. C.—Mesial view of left hemisphere.

Fig. D.—Lateral view of left hemisphere.

Fig. E.—Mesial view of right hemisphere.

Fig. F.—Lateral view of right hemisphere.

The left hemisphere in figs. A, B, C, D is shaded to show the superficial extent of the different types of cortex described. The lettering on the right hemisphere in figs. A, B, E, and F refers to the fissures, while the numbers show approximately the position from which the strips of cortex drawn in figs. 1–13 are taken. These drawings were, many of them, taken from the left hemisphere, but their position has for the sake of simplicity been transferred to the right hemisphere in the diagrams.

FS. Sylvian fissure. *c.* Sulcus centralis. *arc.* Sulcus arcuatus. *it.* Sulcus inferior transversus. *rect.* Sulcus rectus. *fs. 1, 2, 3, 4.* Sulcus precentralis superior and sulcus frontalis superior. *orb.* Sulcus orbitalis. *fo.* Sulcus fronto-orbitalis. *Ts.* Sulcus temporalis superior. *Tm.* Sulcus temporalis medius. *pcs.* Sulcus post-centralis superior. *ip.* Sulcus intra-parietalis. *rpo.* Ramus parieto-occipitalis of sulcus intra-parietalis. *fpo.* Fissura parieto-occipitalis. *sp.* Sulcus subparietalis. *Sc.* Sulcus cinguli. *ro.* Sulcus rostralis. *Col.* Sulcus collateralis. *rh.* Sulcus rhinalis. *lun.* Sulcus lunatus. *oi.* Sulcus occipitalis inferior. *ol.* Sulcus occipitalis lateralis. *Cal.* Sulcus calcarinus.

Magnification in figures 1–13 = 130.

EXPLANATION OF SHADING IN FIGURES A, B, C, D, PLATE 24.
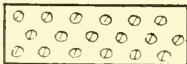
Precentral cortex (Pl. 25, fig. 1).

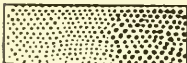Anterior precentral cortex (Pl. 25, fig. 2).
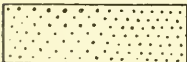
Frontal cortex (Pl. 26, fig. 3).
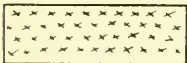
Prefrontal cortex (Pl. 26, fig. 4).

Posterior orbital cortex (Pl. 27, fig. 5).

Post-central cortex (Pl. 27, fig. 6).
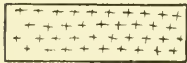
Superior parietal cortex (Pl. 28, fig. 7).

Inferior parietal cortex (Pl. 28, fig. 8).

Calcarine (visual) cortex (Pl. 29, fig. 9).
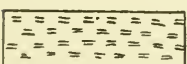
Occipital cortex (Pl. 29, fig. 10).

Temporal cortex (Pl. 30, fig. 11).

Anterior limbic cortex (Pl. 30, fig. 12).

Posterior limbic cortex (Pl. 29, fig. 13).

Olfactory cortex (Pl. 24, fig. E. *rh*, and fig. C).

PLATE 25.

The shading on figs. A. B. C. D in Pl. 24. as shown in the diagram on the opposite page, corresponds in position to the sections of cerebral cortex shown in the several figures in Pls. 25 to 30.

Fig. 1.—Precentral motor cortex.

Fig. 2.—Anterior precentral cortex.

PLATE 26.

Fig. 3.—Frontal cortex.

Fig. 4.—Prefrontal cortex.

PLATE 27.

Fig. 5.—Posterior orbital cortex.

Fig. 6.—Posterior central cortex.

PLATE 28.

Fig. 7.—Superior parietal cortex.

Fig. 8.—Inferior parietal cortex.

PLATE 29.

Fig. 9.—Calcarine (visual) cortex.

Fig. 10.—Occipital cortex.

Fig. 13.—Posterior limbic cortex.

PLATE 30.

Fig. 11.—Temporal cortex.

Fig. 12.—Anterior limbic cortex.